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Variability of coastal cephalopods in overexploited China Seas under climate change with implications on fisheries management

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ABSTRACT

Cephalopods (squids, cuttlefish and octopus) have increased globally over the past decades, which may be attributed to their strong phenotypic plasticity, allowing them to adapt quickly to a changing ocean environment. The global proliferation of cephalopods may yield important ecosystem effects worldwide. However, information on cephalopods variability in Chinese waters is still scant. Coastal cephalopods, in spite of chronic overexploitation, form a vital component of the catch composition in China Seas. In this paper, we review the status and trends of coastal cephalopods in China Seas and explore their responses to environmental variability. We focus on four commercially-important coastal cephalopod species, including golden cuttlefish (*Sepia esculenta* Hoyle), Japanese loligo squid (*Loligo japonica* Steenstrup), common Chinese cuttlefish (*Sepiella maindroni* de Rochebrune) and swordtip squid (*Uroteuthis edulis* Hoyle). Even though spatial distributions of these four species partially overlap, their differing life history strategies with respect to factors such as growth, distribution, migration, and spawning patterns, have led to differing population responses to environmental variability. As a result, an overall increasing trend in cephalopod production has been apparent since the 1990s, accompanied by major changes in species composition. Catch trends of the four species show either decadal patterns of significant decline or increase in the late 1980s to mid-1990s. Statistical analysis indicates different responses to environmental warming, with Japanese loligo squid and swordtip squid seeming to benefit from warmer environment while golden cuttlefish and common Chinese cuttlefish seeming to respond negatively. Our study has allowed us to explore the impacts of environmental changes on Chinese coastal cephalopods in the overexploited ecosystems of the China Seas and to conclude that fluctuations of coastal cephalopods are mainly driven by large scale environmental variations associated with climate change and/or marine ecosystem regime shifts.

1. Introduction

Total world catch production by marine fisheries has maintained an unprecedentedly high level in recent decades. This has been facilitated by dramatic increases in the yield of cephalopods (Ye and Cochrane, 2011; FAO, 2016). As shown in Fig. 1, elevated cephalopod catch coincides with a reduction of global fish stocks (Anderson et al., 2011; Pauly and Palomares, 2005). Cephalopods were found contributing to fisheries in 28 marine ecosystems of the world both in terms of their value as commodities and in terms of the ecological support services they render (Hunsicker et al., 2010; Xavier et al., 2015). Recent evidence has shown that cephalopods in both coastal and oceanic areas have taken advantage of changing ocean environments and have increased in abundance (Doubleday et al., 2016). Although some cephalopod stocks have been overexploited (Quetglas et al., 2015; Tang and Wu, 1986), cephalopods in general appear to withstand substantial expansion in fishery landings, and harvests of cephalopods can be expected to meet ongoing exploitation needs for marine fisheries resources (Arkhipkin et al., 2015).

Impacts of climate change over the past decades have been well documented in the North Pacific Ocean (Sugimoto et al., 2001; McGowan et al., 1998). The 1976/77 regime shift in the North Pacific was commonly recognized as a shift from “negative” to “positive” phase in PDO (Pacific Decadal Oscillation), resulting in significant changes in

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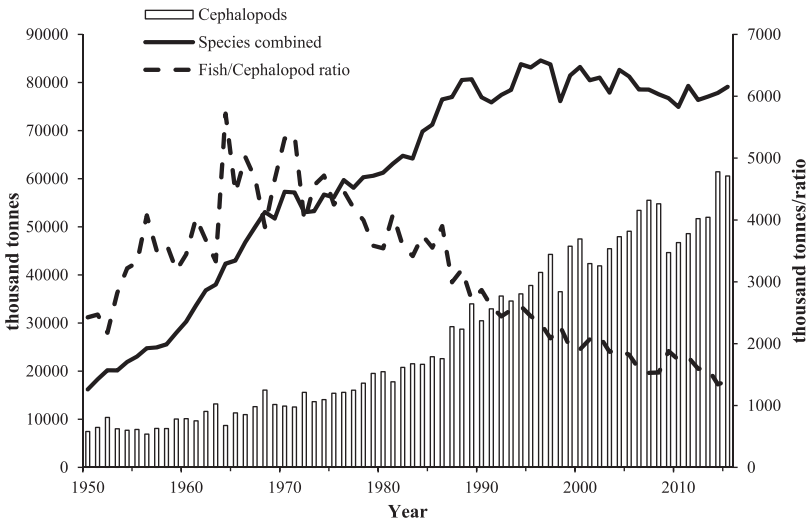

Fig. 1. Global marine catches of species combined (Marine fishes, Crustaceans and Molluscs) (solid line) and cephalopods (squid, cuttlefish and octopus) (bar), and fish to cephalopods catch ratio (100%, dashed line). Global marine catch of species combined was plotted along the first axis, while cephalopods catch and fish/cephalopod ratio along the secondary axis.

environmental conditions (Hare and Mantua, 2000). In addition to the 1976/77 regime shift, annual anomalies of climatic indices indicated a changing thermal regime that subsequently impacted large marine ecosystems of the North Pacific in the late 1980s (Tian et al., 2008). These climatic changes have large impacts not only on individual species such as sardine and squid but also on communities and ecosystems (Chavez et al., 2003: Lehodey et al., 2006; Tian, 2009; Tian et al., 2008, 2013).

Because of their typical biological traits of cephalopods, such as rapid growth, short lifespan, high turnover rate and strong phenotypic plasticity, their growth, maturation and distribution are heavily affected by environmental variation (Pecl and Jackson, 2008; Pierce et al., 2008; Pecl et al., 2004). While coastal ecosystems are easily degraded by high fishing pressure and climate change, cephalopods tend to take advantage of changing environmental conditions and may overtake fish species due to their flexible life history strategies (Caddy and Rodhouse, 1998; Pecl and Jackson, 2008). Thus, cephalopod catch fluctuations in overexploited ecosystems might in large part be driven by environmental variation (Caddy and Rodhouse, 1998). Previous studies on various cephalopod species suggested that climate change significantly influenced status and spatial distributions of cephalopods (Pecl and Jackson, 2008; Sakurai et al., 2000). For instance, stock status and spatial distribution of Japanese common squid (*Todarodes pacificus* Steenstrup) appeared to vary under different thermal regimes (Sakurai et al., 2000). The relative abundance of spear squid (*Loligo bleekeri* Keferstein) in Japanese water showed latitudinal differences and appeared to be primarily driven by major ecosystem regime shifts (Tian, 2009; Tian et al., 2013).

China Seas (Fig. 2) represent a set of overexploited coastal ecosystems where commercial fish stocks have largely declined and individual fish tend to be small-sized and of low-quality due to several decades of high fishing pressure (Ren et al., 2005; Watson and Pauly, 2001). In addition, China Seas is one of the most rapidly warming large marine ecosystems in the world ocean. Sea surface temperature (SST) in the East China Sea increased by 1.22 °C between 1982 and 2006 (Belkin, 2009), evidently associated largely with global warming and large-scale climate variability (Cai et al., 2015, 2014). Consequently, fisheries catch composition and the structure of the ecosystem have changed drastically with fish species declining and invertebrates increasing (Jin and Tang, 1996; Jin, 2004; Liu et al., 2015). Extensive research has been carried out to investigate the impacts of environmental changes on population dynamics and spatial distributions of oceanic cephalopods in the northwestern Pacific (Chen et al., 2008; Sakurai et al., 2002; Yu et al., 2015). However, holistic information on the status of Chinese coastal cephalopods including catch trends and species composition is

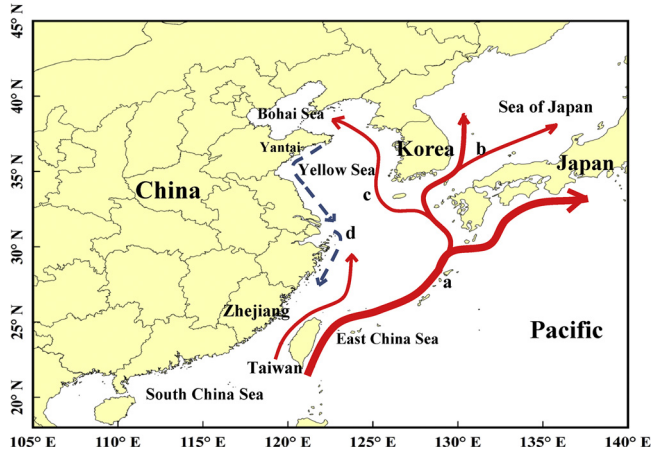

Fig. 2. Map of China Seas (Bohai Sea, Yellow Sea, East China Sea, and South China Sea) and the different currents (a. Kuroshio Current, b. Tsushima warm current, c. Yellow warm current, and d. Mainland coastal current) (Guan, 1994).

scant, and potential influencing factors for population fluctuations are still not well understood.

In this paper, firstly we present a review on the status and variation patterns of Chinese cephalopods over several decades in the context of climate change, with particular focus on four commercially-important, representative coastal species exhibiting different life history strategies: golden cuttlefish (*Sepia esculenta* Hoyle), Japanese loligo squid (*Loligo japonica* Steenstrup), common Chinese cuttlefish (*Sepiella maindroni* de Rochebrune) and swordtip squid (*Uroteuthis edulis* Hoyle). Secondly, we hypothesize that environmental changes have exerted the greatest impacts on coastal cephalopods in the overexploited China Seas and apply statistical analyses to identify oceanographic and climatic factors that influence the dynamics of their populations. Finally, we discuss the relative impacts of environmental changes and human activities on their population fluctuations and attempt to provide useful guidance as to appropriate fisheries management actions under climate change.

2. Materials and methods

2.1. Fishery data and species selection

Data were extracted from various sources at different scales in order to characterize the role of coastal cephalopods through comparisons of cephalopods to fish and oceanic cephalopods to coastal cephalopods

Table 1
Information on fisheries data used in this study.

Scale	Species	Period	Fishing area	Data source
World	fish/cephalopod	1950–2014	All marine area	FAO
Country	fish	1979–2015	China Sea	Chinese annual fishery report (Anonymous, 2015)
	pelagic cephalopod	1950–2015	Far East/USA/ Philippines	Sea around us (www.seaaroundus.org)
	coastal cephalopod	1979–2015	China Sea	Chinese annual fishery report
Region	*Sepia esculenta* Hoyle	1980–1998	Korean water	Korean annual fishery report (Anonymous, 1998)
		1954–2006	Japanese water	Japanese annual fishery report
	Loligo japonica Steenstrup	1960–1984	Bohai Sea/ Yellow Sea	Yantai fishery cooperation (Qiu, 1986)
	Sepiella maindroni de Rochebrune	1958–2010	East China Sea	Zhejiang annual fishery report
	Uroteuthis edulis Hoyle	1960–2005	Taiwanese water	Torchlight fishing vessel in Taiwan (Wang et al., 2008)
		1988–2014	southern Sea of Japan	Japanese annual fishery report (abchan.fra.go.jp)

(Table 1). Total catch of cephalopods, including both oceanic and coastal species, were collected from “sea around us” (www.seaaroundus.org) and Chinese National Fisheries Statistics Yearbook (Anonymous, 2015), respectively. Three major species of oceanic cephalopods, Japanese common squid (*Todarodes pacificus* Steenstrup), Argentina shortfin squid (*Illex argentinus*Castellanos) and Jumbo flying squid (*Dosidicus gigas* Orbigny) were identified at species level. Coastal cephalopods were not identified to species level and were thus grouped together. In addition, we calculated the ratio of coastal cephalopods to fish for different coastal areas, Bohai Sea and Yellow Sea, East China Sea, and South China Sea.

The four coastal cephalopods (i.e., golden cuttlefish, Japanese loligo squid, common Chinese cuttlefish, and swordtip squid) that we choose to focus on in this study have been exploited over six decades in the China Seas. Although spatial distributions of these four coastal cephalopods partly overlap (Fig. 3), life history strategies, such as growth, vertical distribution, migration and spawning patterns, are diverse (Table 2). These diverse biological characteristics potentially may result in great differences in population dynamics under environmental changes.

Fishery data for these four coastal cephalopods, including fishing areas, fishing time and catch, were obtained from published governmental fishery records or local fishery logbooks (Li et al., 2011a, 2011b; Wang et al., 2008; Yan, 1981). Annual catch data for golden cuttlefish are available in Korea (Anonymous, 1998) and Japan (abchan.fra.go.jp), but no accurate data exists for China Seas owing to poor cephalopod species identification. Catch data for Japanese loligo squid were derived from logbooks of a local fishery company in Yantai, Shandong Province prior to 1983 until filefish (*Thamnaconus modestus* Günther) became a major targeted species (Yan, 1981). Exploitation of common Chinese cuttlefish started earlier than recorded in Chinese official fisheries documentation. The main fishing ground is located at Zhoushan Island in the East China Sea. Accordingly, we used data from Zhejiang Province fisheries records to represent its catch in East China Sea (Wu et al., 2010). Catch data for the northern population of swordtip squid in Sea of Japan were collected from the Japan Fishery Agency (abchan.fra.go.jp) and relevant catch data in northeastern waters of Taiwan were obtained from published research on a “southern population” (Wang et al., 2008). Due to the lack of CPUE and other more accurate abundance indices for the four coastal cephalopods, we used catch as a proxy for relative abundance in the following statistical analyses. We consider this proxy reasonable because of the non-selective and no-discards nature of fishing operations in the China Seas (Chen, 2001; Liu, 2004).

2.2. Water temperature data and climatic indices

Sea surface temperature is an important oceanographic variable that relates to ocean circulation patterns, vertical mixing, availability of nutrients, and subsequent marine ecosystem primary production, which appears to be the leading indicator and important driver in marine fisheries resource fluctuations (Ottersen et al., 2010). SST data for China Seas were taken from the Met Office Marine Data Bank, which also includes data received from the Global Telecommunications System since 1982 (Rayner et al., 2003). SST data for Japanese water were provided by Japan Meteorological Agency, which is more local. Since the data set consists of monthly global fields of SST on a one-degree latitude-longitude grid, we calculated annual average SST for the four areas of China Seas to search for temporal trends. Moreover, seasonal/monthly SST anomalies are often applied to examine correlations with stock fluctuations in long term trends (Gordoa et al., 2000; Robin and Denis, 1999; Tian et al., 2004), thus average SST in spring (April–June), summer (July–September), autumn (October–December) and winter (January–March) were also calculated for statistics analysis in this study. SST anomalies in summer and winter were plotted for comparison purpose.

In addition to local SST, well-documented large-scale climatic indices including PDO, AO (Arctic Oscillation), SOI (Southern Oscillation Index) and MOI (Asian Monsoon Index), can also act as proxies for environmental variations that impact marine fisheries resources (Hays et al., 2005; Mantua and Hare, 2002; Maynou, 2008; Tian et al., 2004; Tian, 2009; Tian et al., 2013), and have thus been obtained for statistical analysis in this study.

2.3. Statistics analysis

A sequential *t*-test analysis of regime shifts (STARS) was applied to the catches of these four coastal cephalopods, an approach commonly used to describe step-changes of catch with a long time series (Friedland and Hare, 2007; Rodionov, 2004; Tian, 2009).

Generalized additive models (GAMs; Hastie and Tibshirani, 1990) were applied to model the influence of four seasonal SSTs and climatic factors on the catch trends of cephalopod populations. Before conducting GAMs, all the catch data were standardized by subtracting the mean and dividing by the standard deviation. This standardization allows all the catch data to be expressed on the same scale and with the same spread. Corresponding environmental variables were assigned to different populations based on their habitats and distributions. For populations of golden cuttlefish in Japan and Korea, SST in the southern Sea of Japan and Yellow Sea, respectively, were selected. SST data in Bohai Sea were used for Japanese loligo squid, data in the East China Sea were used for both common Chinese cuttlefish and swordtip squid. SST data in the southern Sea of Japan were applied to swordtip squid occurring in Japanese waters.

To avoid collinearity and for consistency, area- and population-specific time series of standardized catch were modelled as smoothing functions of a single environmental variable (using a subset of the data as training dataset (i.e., excluding the last 3 years of the annual time series with length N):

$$C_t = \alpha + s(V_t) + \varepsilon_t, \quad t = 1, \ldots, N-3$$

where C_t is the response variable representing standardized annual catch of different cephalopod species, predictor variable V_t refers to environmental variables, $s()$ is the smoothing function, α is the

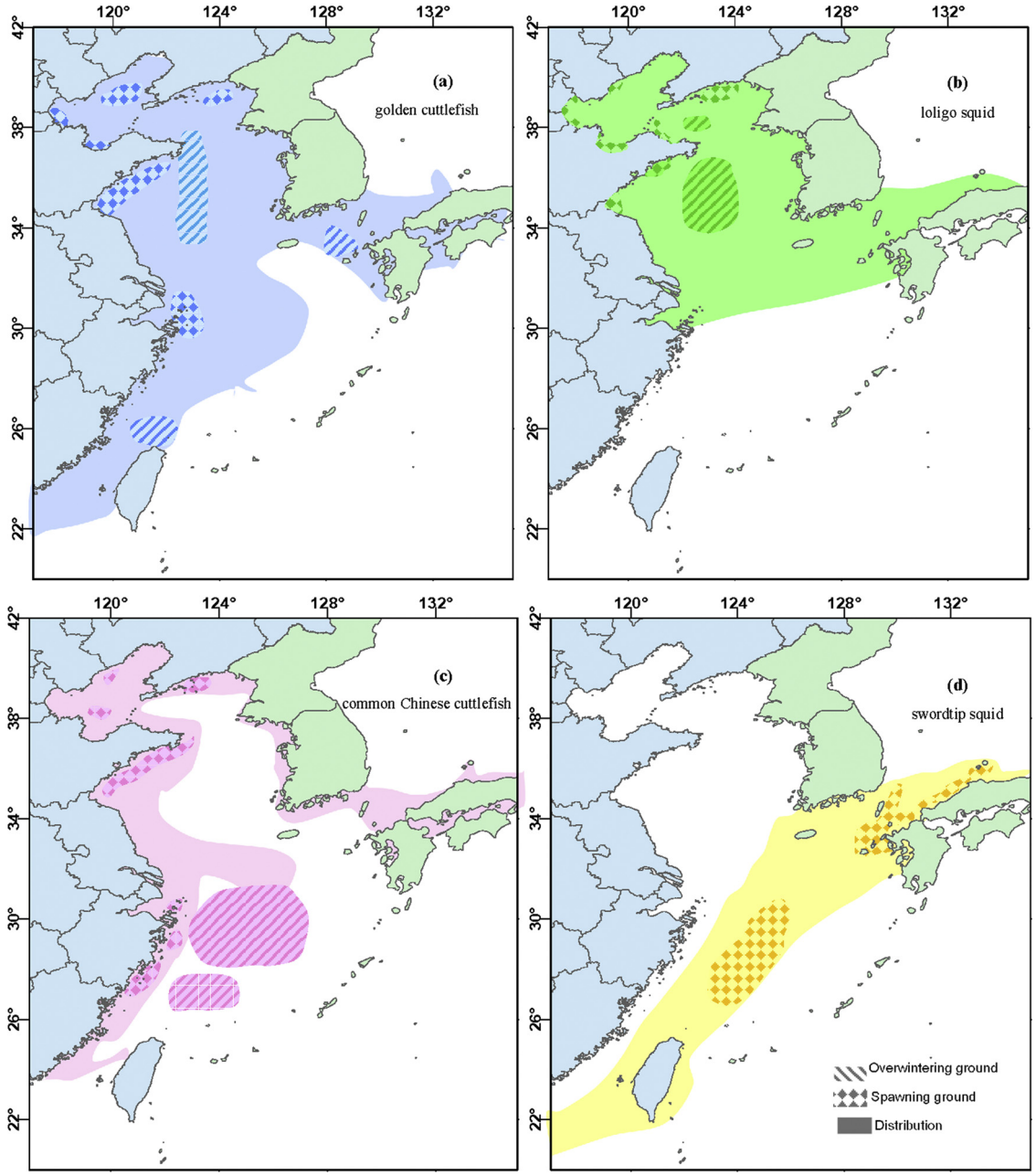

Fig. 3. Schematic distributions of four coastal cephalopods in the China Seas (references listed in Table 2): (a) golden cuttlefish (*Sepia esculenta* Hoyle), (b) Japanese loligo squid (*Loligo japonica* Steenstrup), (c) common Chinese cuttlefish (*Sepiella maindroni* de Rochebrune), and (d) swordtip squid (*Uroteuthis edulis* Hoyle).

intercept of the model, and ε is the random error term of normal distribution with zero mean and finite variance. The underlying statistical assumptions were tested through graphical residual analyses. To avoid over-fitting, the effective degrees of freedom (edf; representing the level of non-linearity) are restricted to a maximum of 4. In the presence of significant temporal auto-correlation, Generalized Additive Mixed Models (GAMMs; Pinheiro and Bates, 2000) were used to include residual auto-correlation structures. Auto-regressive (AR) models of order 1 or 2 as well as auto-regressive moving average (ARMA) models with different combinations of order 1 and 2 were compared and the best error structure was chosen based on the Akaike's Information Criterion (AIC; Zuur et al., 2009). The quality of a model resulting from the training dataset was assessed by how well the model predicted the test dataset (i.e., the last 3 years) using the normalized root mean square error (NRMSE) on the test dataset.

In the case of non-linear responses of catch to environmental variables, we examined the first derivative of the smoothing function, denoted as s'(*V*), representing the instantaneous change rate of catch to that of the environmental variable. Confidence intervals (*CI*) of the first derivative were generated by carrying out a conditional bootstrap by resampling from the GAM residuals. The catch response to environmental changes was considered not to be statistically significant when zero is contained within the *CI* of the first derivative.

Threshold GAM (TGAM; Ciannelli et al., 2004) was applied to detect interactions between two environmental variables, an approach that is particularly useful if changes in response to the interacting environmental variables are step-wise. GAM and TGAM models were compared and the best model was determined by using the genuine cross-validation squared prediction error criterion. For those cephalopod species that manifested interactions between two environmental variables, all relevant plots from the statistical analysis have been provided for demonstration purposes. All the calculations were done according to Otto

Table 2
Biological traits and fishery of four cephalopods.

Species	Maximum size	Environmental/ climate range	Migration & Ecology	Spawning season	Fishery
golden cuttlefish (*Sepia esculenta* Hoyle)	180 mm/600 g	Demersal, Eurythermal species	Overwinter in deep water and migrate to shallow water spawning in spring	Between spring and early summer along coastal areas	Targeted species in Yellow Sea before 1980s then replaced by octopus. Resources recovering by artificial releasing[a]
Japanese loligo squid (*Loligo japonica* Steenstrup)	120 mm/76 g	Pelagic, cold water species	Shallow-deep water migration, easily affected by extreme weather	May in north of China Seas	Fishing happens mainly in Bohai Sea and Yellow Sea. Keep great abundance with seasonal variablity in coastal area in recent years[a]
common Chinese cuttlefish (*Sepiella maindroni* de Rochebrune)	200 mm/800 g	Demersal, warm water species	Shallow-deep water migration, being selective to spawning habitats	April to June off Japan and East China Sea	Highly-valued with an average catch of 45,000 tons/yr in East China Sea until collapse in the 1980s. No signs of recovery up to now
swordtip squid (*Uroteuthis edulis* Hoyle)	400 mm/820 g	Pelagic, warm water species	Migration is driven by Kuroshio Current and coastal currents in East China Sea	All year round but with two distinct spawning seasons (spring & autumn) in East China sea	Annual catch still remains about 10,000 tons in the 2000s in Taiwan

Reference: golden cuttlefish (Hao et al., 2007; Li, 1963; Wei et al., 2005); Japanese loligo squid (Ge and Qiu, 1991; Qiu, 1986; Yan, 1981); common Chinese cuttlefish (Li et al., 2011a, 2011b; Ni and Xu, 1982; Tang and Wu, 1986; Wu et al., 2010); swordtip squid (Wang et al., 2013, 2010, 2008; Yamaguchi et al., 2015).
[a] Unpublished data from fishery-independent surveys in Haizhou Bay, Yellow Sea during 2011–2016.

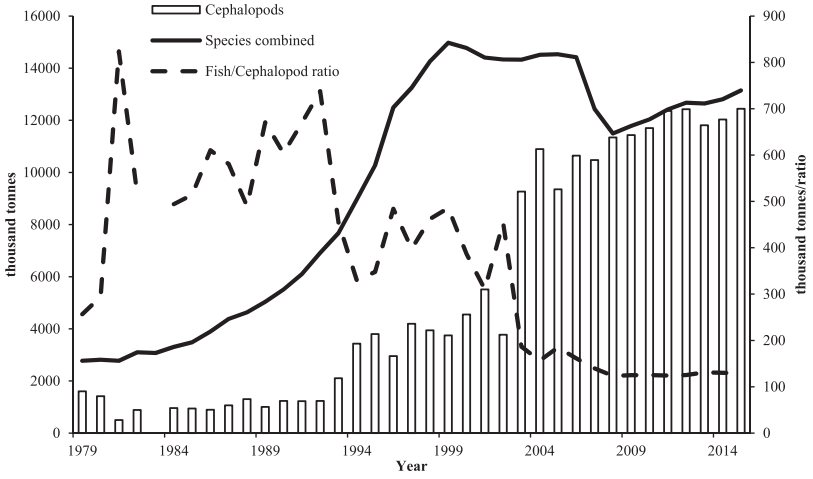

Fig. 4. Chinese coastal catches of species combined (Marine fishes, Crustaceans and Molluscs) (solid line) and cephalopods (squid, cuttlefish and octopus) (bar), and fish to cephalopods catch ratio (10%, dash line, data of cephalopod in 1983 missing). Chinese coastal catches of species combined was plotted along the first axis, while cephalopods catch and fish/cephalopod ratio along the secondary axis.

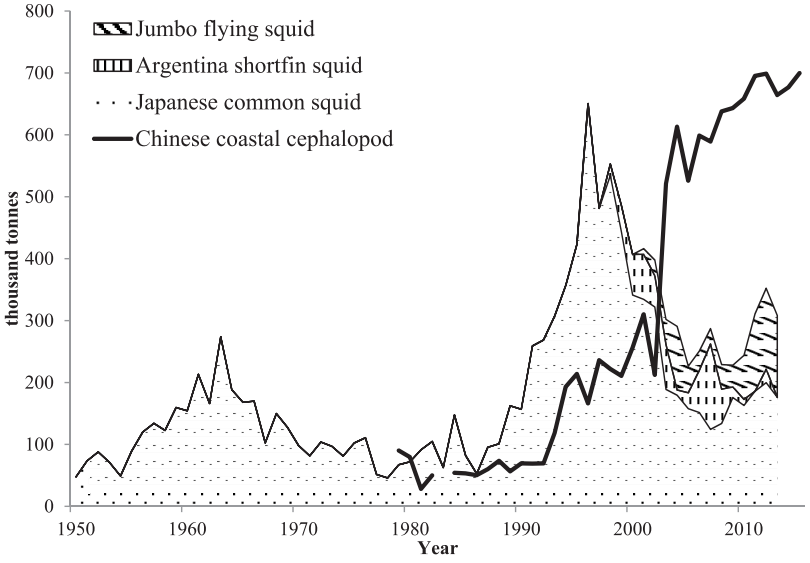

Fig. 5. Catches of Chinese coastal cephalopods (data in 1983 missing) and major oceanic cephalopods.

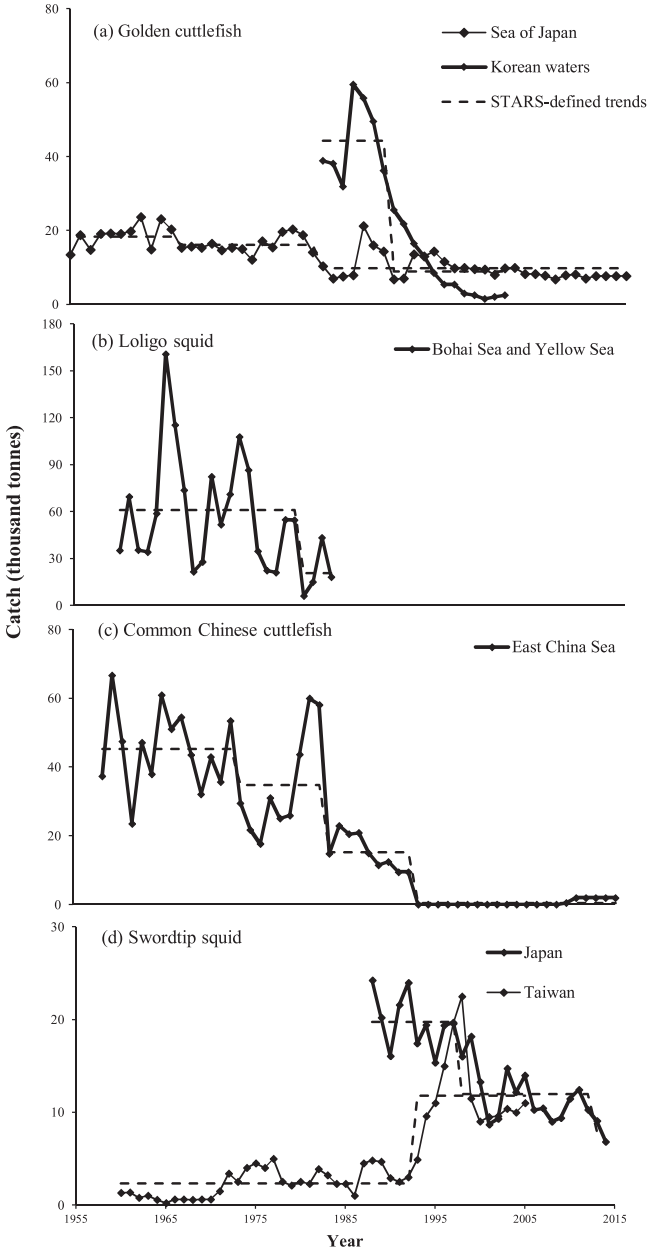

Fig. 6. Catches (solid lines) of four coastal cephalopods in the China Seas: (a) golden cuttlefish, (b) Japanese loligo squid, (c) common Chinese cuttlefish, and (d) swordtip squid. Step changes based on a sequential *t*-test analysis of regime shifts (STARS-defined trends) for catches are shown by dashed lines.

et al. (2018a) using the package 'INDperform' (Otto et al., 2018b) within the R environment (R Core Team, 2017).

3. Results

3.1. Status and variations of Chinese cephalopods

Similar to the global catch trends of fish and cephalopod species (Fig. 1), catches of coastal cephalopods in China seas show an increasing trend since the 1990s while total fish catch declined after the mid-2000s (Fig. 4). The ratio of fish to cephalopods caught varied substantially but kept decreasing from larger than 600 during the 1980s to below 200 during the 2000s, and significant declines occurred around 1990 and 2000.

Catches of both coastal and oceanic cephalopods increased after 1990 in China (Fig. 5), showing a similar trend to that of the global cephalopods catch (Fig. 1). However by the mid 1990's, catches of oceanic cephalopods declined, while catches of coastal cephalopods kept increasing. Japanese common squid has a long history of being exploited in China Seas by foreign countries (mostly by Japan), showing two great peaks during the early 1960s and the late 1990s. With improvements in fishery technologies in the 1980s, China began to develop pelagic fisheries for oceanic cephalopods such as Jumbo flying squid and Argentina shortfin squid, and increased its exploitation rate on Japanese common squid in coastal areas. Oceanic cephalopods played a vital part in contributing to total cephalopod production in China until 2000, when the catch of coastal cephalopods started to outweigh that of oceanic cephalopods with an increasing trend reaching around 700 thousand tons (Fig. 5).

3.2. Catch trends of four coastal cephalopods

The catches of the four coastal cephalopods showed large fluctuations at different time scales, often with step changes (Fig. 6). No Chinese catch data is available for golden cuttlefish. The catch of golden cuttlefish presented a sharp decline around 1985 in Korean water (mostly in Yellow Sea); whereas the catch from the Sea of Japan gradually decreased in the 1980s to nearly half of that before 1960 (Fig. 6a).

The catch of Japanese loligo squid fluctuated greatly in a cyclic pattern in Bohai Sea and Yellow Sea, with a maximum catch of 160 thousand tons in 1965. However, average catch reduced to less than 40 thousand tons around 1975. With the fishery target switching to high valued filefish, no catch statistics were available for Japanese loligo squid after 1983 (Fig. 6b).

The catch of common Chinese cuttlefish from the East China Sea showed large inter-annual variations with high catch production before the 1960s followed by a decreasing trend in the 1970s and an abrupt collapse after the mid-1980s. Even though hatchery releases have been tried for cuttlefish, no signs of recovery were found in the natural population of this species (Fig. 6c).

Whereas the population of common Chinese cuttlefish suddenly collapsed in the mid-1980s in East China Sea, the catch of swordtip squid increased continuously in the 1990s (Fig. 6d). On the other hand, data showed a significant decline in both the southern (East China Sea) and the northern (Sea of Japan) populations of swordtip squid around 1998/1999.

Overall, catches of these four cephalopod species showed different patterns and varied greatly; significant decreases/increases mainly occurred in the 1980s and 1990s, coinciding with the drastic changes in oceanographic and climatic indices, indicating potential impacts of climate change on the population dynamics of coastal cephalopods.

3.3. Environmental variabilities in China Seas and their impacts on cephalopods

Overall, no significant linear trends were detected in the annual SST in China Seas over the last six decades, although it slightly increased since the 1980s in the southern segments (East China Sea and South China Sea) of the China Seas (Supplementary Fig. S1). On the other hand, winter and summer SSTs showed evidence of decadal variabilities with abrupt changes from cold to warm in winters around the late 1980s and in summers around the mid-1990s (Supplementary Fig. S2), in substantial association with climate indices (Figure not shown). Extremely cold summer and winter occurred in the north of China Seas in 1977 and 1981, respectively (Supplementary Fig. S2a, b).

Significant relationships between catches and environmental variables were found for all four cephalopod species in both Korean and Chinese waters at various statistical significance levels (Table 3). The significant relationship with the highest R^2 (0.55) was found between swordtip squid catch and summer SST in East China Sea, the correlation

Table 3
Best fitted models for coastal cephalopod populations. GAM: generalized additive model, AR1 or AR2: auto-regressive model or order 1 or 2, ARMA11: auto-regressive moving average model of order 1-1, AIC: Akaike information criteria, Environmental drivers include climate indices (PDO: Pacific Decadal Oscillation, SOI: Southern Oscillation Index, AO: Arctic Oscillation, MOI: Asian Monsoon Index) and regional sea surface temperature in summer (SUM), autumn (AUT), winter (WIN), and spring (SPR). Model significance levels include: * ($p < 0.05$), ** ($p < 0.001$), *** ($p < 0.0001$); the effect of a driver on cephalopod catch is either "+" for overall positive, "–" for overall negative, or "○" for highly non-linear or no effect.

(a)

	Golden cuttlefish (Japan) Southern Sea of Japan				Golden cuttlefish (Korea) Yellow Sea				Loligo squid Bohai Sea			
Driver	Model	AIC	p-value	effect	Model	AIC	p-value	effect	Model	AIC	p-value	effect
PDO	GAM	76.80	0.5997	–	AR1	31.75	0.7454	○	GAM	66.59	0.4431	–
SOI	GAM	76.37	0.5957	○	AR1	31.75	0.7433	○	AR1	66.35	0.9173	○
AO	GAM	75.74	0.4505	+	AR1	31.82	0.8342	○	GAM	66.26	0.7560	+
MOI	GAM	72.93	0.1633	+	AR1	31.84	0.8782	○	GAM	65.98	0.5467	–
SUM	GAM	76.34	0.4079	+	AR1	31.35	0.4866	+	GAM	65.72	0.4375	+
WIN	AR2	71.92	0.0267	– *	GAM	46.31	0.0243	– *	AR2	64.01	0.3531	○
AUT	GAM	77.08	0.8971	○	AR1	31.16	0.4216	–	GAM	59.32	0.0200	+ *
SPR	GAM	75.74	0.2683	–	AR1	31.67	0.6694	○	AR1	66.23	0.7281	+

(b)

	Common Chinese cuttlefish East China Sea				Swordtip squid (China) East China Sea				Swordtip squid (Japan) Southern Sea of Japan			
Driver	Model	AIC	p-value	effect	Model	AIC	p-value	effect	Model	AIC	p-value	effect
PDO	GAM	77.51	0.0625	–	AR1	46.71	0.0764	+	AR1	36.05	0.3073	○
SOI	AR1	80.53	0.5826	+	AR1	49.98	0.9914	○	AR1	36.35	0.5504	○
AO	GAM	80.56	0.2332	–	AR1	48.71	0.2722	–	AR1	36.73	0.9561	○
MOI	AR1	72.30	0.0043	– **	AR1	46.18	0.0579	–	AR1	36.21	0.4848	–
SUM	AR1	80.79	0.8052	+	GAM	60.57	0.0005	+ ***	AR1	27.58	0.0034	– **
WIN	AR1	76.95	0.0460	– *	AR1	49.43	0.4500	+	AR1	35.82	0.3538	–
AUT	GAM	76.57	0.0453	– *	ARMA11	41.72	0.0023	+ **	AR1	35.40	0.2605	–
SPR	GAM	80.01	0.2169	–	AR2	31.22	0.0000	+ ***	AR1	34.08	0.1456	–

being a positive one (Table 3b, Fig. 7a). Summer SST was found interacting with autumn SST in the TGAM analysis and the positive relationship between catch and summer SST mostly occurred when the autumn SST anomaly was above 0.5 (Fig. 7e). The catch response to environmental changes was statistically significant with a range of 59% (Fig. 7c). The model fit to the last 3 years was rather good (Fig. 7b). Similar positive curves also appeared in the correlations with spring and autumn SST (Table 3b, Fig. 8a, b). On the other hand, the population of swordtip squid in the southern Sea of Japan was negatively related with summer SST but with a low R^2 (0.08). The catch of common Chinese cuttlefish in East China Sea was negatively correlated with autumn SST at positive anomalies (Table 3b, Fig. 9a) with autumn SST interacting with PDO. The negative response occurred when the PDO anomaly was above 0.48 (Fig. 9e). In addition, negative connections of common Chinese cuttlefish catch were found with both MOI (Table 3b, Fig. 8c) and winter SST (figure is not shown). Loligo squid catch was found to be positively correlated only with autumn SST (Table 3a, Fig. 8d). Both populations of golden cuttlefish in Korean water and the Sea of Japan were in negative relationships with winter SST (Table 3a, Fig. 8e, f).

4. Discussion

4.1. Species-specific response patterns to climate change

Catch trends of the four coastal cephalopod species, available at different time scales, showed different patterns and variations with drastic decreases/increases mainly occurring in the 1980s and the 1990s, indicating potential large impacts of climate change and regime shifts. Different patterns among the four species strongly suggested the species-specific response to climate change, resulting from differences in life history characteristics.

Positive relationships were found between swordtip squid catch and SST in spring, summer, and autumn in the East China Sea. Winter SST in East China Sea tended to rise since the late 1980s (Supplementary Fig. S2) which seems to have significantly accelerated somatic growth rate and to have advanced maturation at small size (Wang et al., 2013, 2010; Yamaguchi et al., 2015). The increase of swordtip squid catch in East China Sea in the 1990s seemed to have been caused not only by high exploitation rates (Park et al., 2002), but also by the favorable warm environment that characterized the regime shift. However, swordtip squid population in the southern Sea of Japan appeared to have been negatively affected by warm summer SST. One possible explanation is that Japanese water constitutes the northernmost distribution of this species, and so catch of swordtip squid declined when environment became warmer than their optimal thermal range during the warmer regime of the 1990s. Nevertheless, the underlying mechanisms are still unclear due to lack of knowledge on the biology and ecology of this population.

Our statistical results indicated that common Chinese cuttlefish catch was negatively related to the rise of autumn SST. Negative effect of MOI was significant on common Chinese cuttlefish through the association with increasing winter water temperature especially when PDO anomalies were positive. The collapse of common Chinese cuttlefish stock in the East China Sea in the late 1980s was considered mainly an outcome of intensive resource exploitation and consequent habitat destruction by bottom trawling (Wu et al., 2010). Nevertheless, a shift to warmer regime in the late 1980s would be expected to have also contributed to the stock collapse. Since our statistical analysis did not include fishing pressure as a driving factor, quantifying the relative impacts of environmental changes and fishing activities on the catch variability before the stock collapse would be difficult.

Populations of golden cuttlefish have relatively low optimal water temperature in both the Korean waters and the Sea of Japan and tend to be distributed in cold water. Thus, warmer environment would affect their growth and development in a negative way (Robinson et al.,

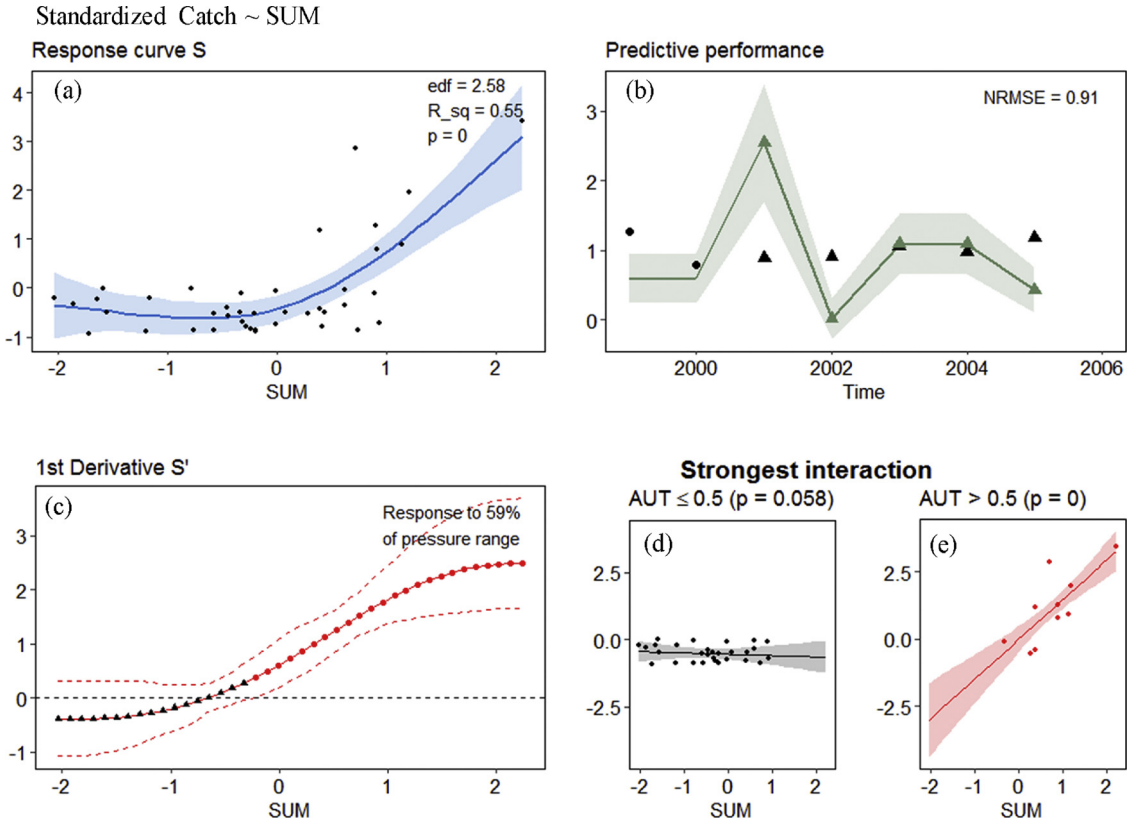

Fig. 7. Results of the best model for swordtip squid in East China Sea: (a) response curve of standardized catch to SUM (sea surface temperature in summer) with edf for effective degree of freedom, R_sq for coefficient of determination representing goodness of fit, p for p-value; (b) first derivative of the smoothing function s (i.e., instantaneous change rate of catch to that of SUM); (c) normalized root mean square error (NRMSE) on the test dataset (i.e., the last 3 years); (d) and (e) are responses of standardized catch to SUM when AUT (sea surface temperature in autumn) is ≤0.5 and > 0.5, respectively. Y-axis is standardized catch.

2013). Our statistical results indicated negative correlations between catches and winter SST. Golden cuttlefish catch in Korea seriously decreased in the late 1980s with the rise of winter SST in Yellow Sea, which was tightly related to the shift from cold to warm regime occurring in the northwest Pacific (Tian et al., 2008, 2013). During the same time, catch declined by almost half for the population in Japanese waters, which might also be influenced by water temperature variation corresponding to the transfer into the positive phase of PDO. Golden cuttlefish migrates to Yellow Sea (overwintering ground) where water temperature gradually decreases. When higher water temperature in the overwintering area occurs, the period of overwintering is shortened which induces an early onset of spawning migration resulting in relatively poor reproductive condition, high marine mortality, and subsequently weak recruitment (Crozier and Hutchings, 2014).

A strong positive relationship was found between loligo squid catch and autumn SST in the GAM model, which implied that warmer environment would accelerate individual growth of cold water loligo squid especially at larval and juvenile stages and thus increase recruitment success and subsequent catch. Since the mid-1970s, catch had been declining and reached its lowest levels in 1977 and 1981. Coincidentally, lowest summer and winter SST in Bohai Sea were recorded in 1977 and 1981, respectively. The suddenly cooling environment may have suppressed the hatching process and reduced the growth and survival of young-of-the-year (Sato et al., 2009), thus resulting in poor fishery performance.

The four species that we explored in this paper are representative of coastal cephalopods in the China Seas, and they serve as good examples of potential linkages between environmental variability and population fluctuations. High turnover rate of cephalopod species, decreasing competitions with fish stocks in the overexploited coastal ecosystems could all have contributed to the booming coastal cephalopods in China Seas. Statistical analysis relating these four species to environmental variables also underscores the influence of climate change like regime shifts.

4.2. Increasing trend in coastal cephalopods under overexploitation

The increasing trend in coastal cephalopods catches (Fig. 4) is consistent with the global trends in cephalopods abundance (Doubleday et al., 2016), and shows tight association with the rise of SST in China Seas in the 1990s (Supplementary Fig. S2), suggesting the potential effects of a changing environment especially global warming on community composition and ecological structure under intensive fishing activities. Study for the northern part of East China Sea showed that environmental changes, especially water temperature variation, substantially affected the biodiversity and ecological structure (Liu et al., 2015). Moreover, the ratio of cephalopod to fish catches portrays declined fish populations and booming cephalopod populations in China Seas (Fig. 4). A number of studies have pointed out that fish species have become less abundant, smaller-sized, and of lower-quality, while invertebrates have become more dominant in the coastal areas of the China Seas (Ren et al., 2005).

In addition to the increases in coastal cephalopods along four coastal areas of the China Seas (Figure not shown), previous scientific surveys have also shown that species composition of coastal cephalopods varied greatly over the last six decades with biodiversity increasing from north to south of the China Seas. While loligo squid has been dominant in Bohai Sea over time (Qiu, 1986), species compositions in Yellow Sea and East China Sea have changed due to persistent fishing activities. Golden cuttlefish was primarily targeted in Yellow Sea until Japanese common squid took its place since the 1980s. When the abundance of these two species deceased after 2000, octopus and

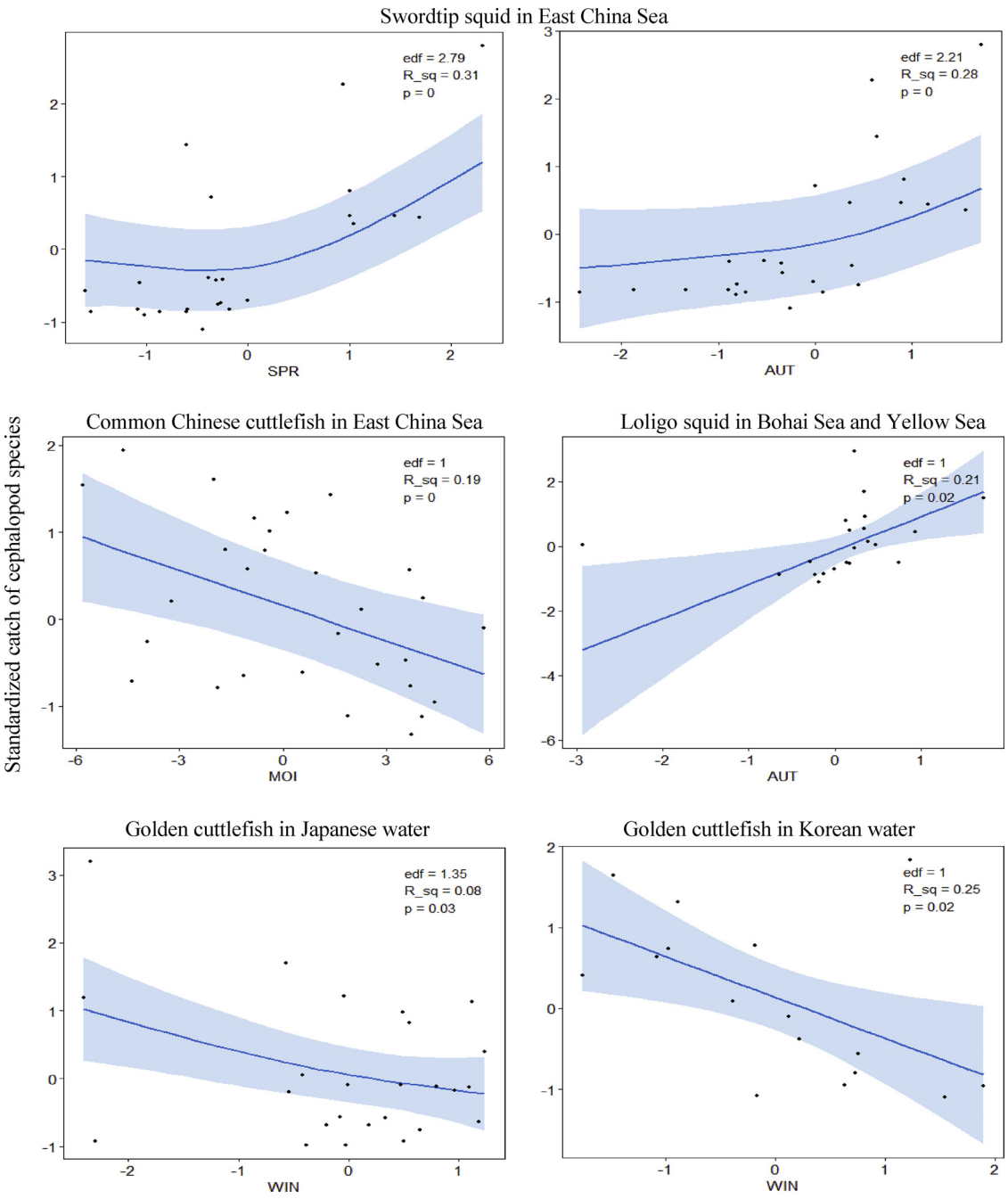

Fig. 8. Catch response curves of (a and b) swordtip squid in East China Sea to SPR (sea surface temperature in spring) and AUT (sea surface temperature in autumn), (c) common Chinese cuttlefish in East China Sea to MOI (Asian Monsoon Index), (d) loligo squid in Bohai Sea and Yellow Sea to AUT; (e) golden cuttlefish in Japanese water to WIN (sea surface temperature in winter), (f) golden cuttlefish in Korean water to WIN.

Sepiolida species of low commercial value occupied the Yellow Sea (Wu et al., 2015).

A similar pattern occurred in East China Sea. As common Chinese cuttlefish nearly collapsed in the late 1970s, substantial Japanese common squid and swordtip squid were landed in the 1990s. Then small-sized cephalopods like kobi cuttlefish (*Sepia kobiensis* Hoyle) began to replace large-sized cephalopods in the 2000s (Zhu et al., 2014). Even though South China Sea has the highest diversity of cephalopods, only a few species are exploited currently including the common Chinese squid (*Loligo chinensis* Grey) and swordtip squid being the main targeted species (Huang, 2008).

Even though detailed information on cephalopod production is limited in the overexploited China Seas, our data review has revealed that total biomass dramatically increased over the last several decades, which might be partly contributed by species such as swordtip squid and loligo squid that seem to have benefited from continually warming of their environment in the last two decades. This is in total agreement with our statistical results that indicated significantly positive relationships between catches and seasonal SST variations. Unpublished data also revealed that these two species maintain great abundance in the coastal areas up to now (Table 2). On the other hand, golden cuttlefish and common Chinese cuttlefish have been less abundant and increasingly replaced by small-sized cephalopods, taxa that lack species identification and long-term records in the data sets but have supported the coastal fishery greatly after 2000 (Yan et al., 2007).

Although limited data prevented us from separating the influence of

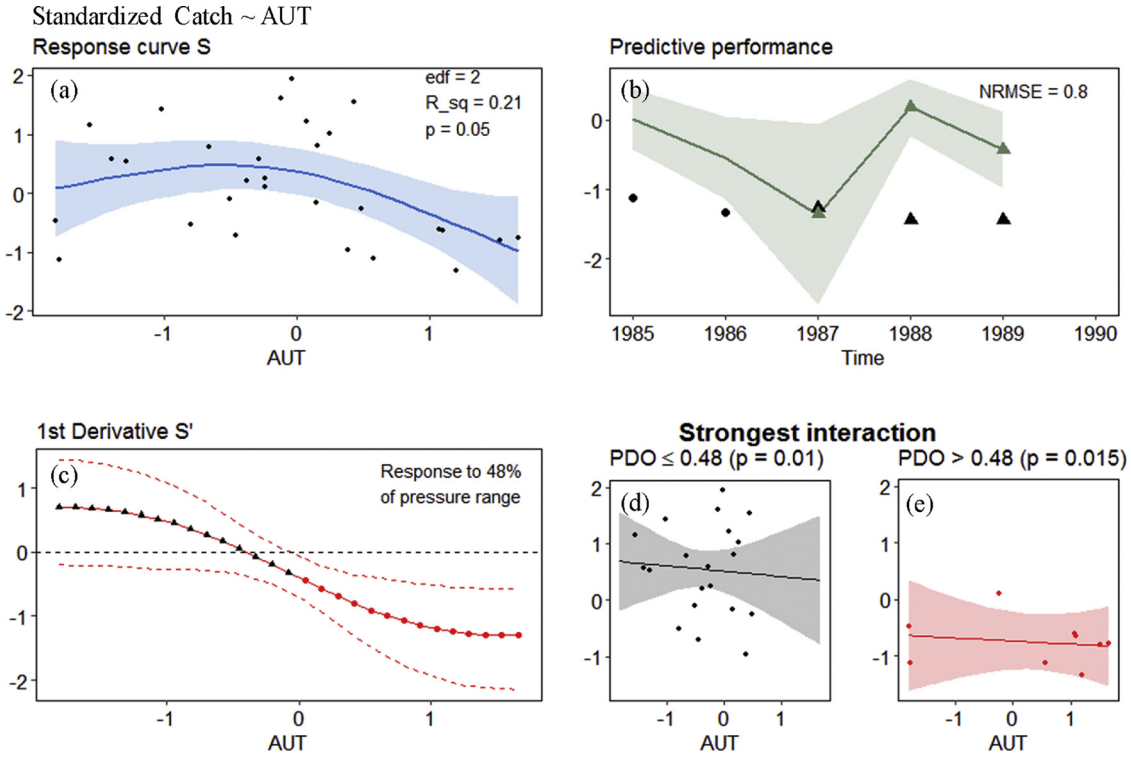

Fig. 9. Results of the best model for common Chinese cuttlefish in East China Sea: (a) response curve of standardized catch to AUT (sea surface temperature in autumn) with edf for effective degree of freedom, R_sq for coefficient of determination representing goodness of fit, p for p-value; (b) first derivative of the smoothing function s (i.e., instantaneous change rate of catch to that of AUT); (c) normalized root mean square error (NRMSE) on the test dataset (i.e., the last 3 years); (d) and (e) are responses of standardized catch to SUM (sea surface temperature in summer) when PDO (Pacific Decadal Oscillation) is ≤0.48 and > 0.48, respectively. Y-axis is standardized catch.

environmental changes from fishing activities in the China Seas, we have demonstrated that coastal cephalopods, in contrast to the concurrent serious declines in the abundance of fish species, displayed positive response to environmental changes in reflection of their life history flexibility and quick adaptation to changing environment (O'Dor, 1998; Pierce et al., 2008). Our results are in agreement with those for other degraded ecosystems in West Africa, Gulf of Thailand and Adriatic, suggesting that long-time fishing pressure and activities have changed ecological conditions, and that cephalopods have taken advantage of vacant ecological niches to increase their populations while fish stocks have declined (Caddy and Rodhouse, 1998).

4.3. Implications for fisheries management of coastal cephalopods in the China Seas

Nowadays, cephalopods are increasing their importance as both commercially-important fishery resources and ecological support service in the China Seas ecosystems (Fig. 4 and Table 2). In the China Seas, multi-species bottom trawling, an important fishery mode, has posed serious threats to benthic habitats and larval survivorship of cephalopods (Tang and Wu, 1986). The only measure applied for fishery management in the China Seas is a summer fishing moratorium from May to August (Lin and Cheng, 2009), which is too general to manage at the same time various species possessing diverse life histories. For instance, the wild population of benthic common Chinese cuttlefish has showed no signs of recovery in the East China Sea in spite of much effort on hatchery releases, an apparent result of serious destruction of benthic cephalopod habitats by commercial bottom-trawl fishing. In contrast, pelagic species such as swordtip squid responded positively to both a warming environment and increasing fishing activities; its resource fluctuation would seem to be mainly driven by environmental changes, since bottom trawling would not largely affect its habitat and early life stages.

Given the unique biological characteristics of cephalopods, traditional stock management strategies for fish species cannot be assumed to be applicable to coastal cephalopods in the context of climate change (O'dor, 1998; Pierce and Guerra, 1994). External factors like environment and human activities can contribute to stock fluctuations; however, it is their diverse life history patterns that determine how coastal species would respond diversely to climate change. Hence, to set up ecosystem-based fishery management that specifically incorporates climate change for coastal cephalopods, it is indispensable to have a good understanding of life history traits of different species, to foresee the potential influence of environmental changes and human activities and to put forward precautionary measures for sustainable fisheries management.

Moreover, for the purpose of rebuilding or restoring an overexploited ecosystem, the ecological roles and population resilience of different coastal cephalopods deserve further research under overexploitation. China Seas would serve as typical and easily-monitored case studies for learning about coastal cephalopods. Combining researches of population dynamics with studies on ecological function, we hope to provide guidance for making good use of coastal cephalopods in a sustainable way, thereby avoiding the tragedy of collapse that fish species have experienced.

4.4. Conclusions

The increase of total coastal cephalopods in the overexploited China Seas was in remarkable consistence with the world-wide booming of cephalopods under climate change especially global warming, in spite of the fact that some cephalopod stocks have declined or even collapsed. Catch trends of four commercially-important Chinese coastal cephalopods on different time scales showed significant population

fluctuations in the 1980s and 1990s. Statistical results on the correlations of cephalopod stocks with environmental factors indicated that coastal cephalopods in China Seas were largely affected by regime shifts and climate change through seasonal SST variations. Different responses to environmental variations were found for different species due to their diverse life history characteristics. Coastal cephalopod stock fluctuations were mainly driven by environmental changes in the China Seas where intensive fishery activities have taken place over the last several decades. Species-specific measures of fisheries management should be vigorously enforced with respect to Chinese coastal cephalopods in the overall context of their overexploited and degraded ecosystem.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2018.07.004.

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